The epiphytic bryophyte community of Atlantic oak woodlands shows clear signs of recovery following the removal of invasive *Rhododendron ponticum.*

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Abstract

Increased awareness of the negative impacts of invasive non-native species has led to a rapid increase in clearance programs around the world. One of the main goals of clearance is the restoration of native communities that were present pre-invasion. Little monitoring is typically carried out, however, to verify that native communities return without further management intervention in the years following invasive species removal. We investigated whether the epiphytic plant community of Atlantic oak woodlands, which principally consists of bryophyte species, returned after up to thirty years of recovery following the removal of the invasive non-native shrub *Rhododendron ponticum*. This community is of international conservation value and is particularly threatened by invasive *Rhododendron*. We revealed that the epiphytic plant community was able to recover effectively in sites that had been clear from *Rhododendron* for over fifteen years. This recovery included several species of particular conservation interest with highly restricted European distributions (i.e. 'Atlantic species' such as *Plagiochila heterophylla*). Total cover and species richness both returned to similar or even higher levels to those found in uninvaded control plots by fifteen or more years following clearance, despite being highly reduced within dense *Rhododendron* thickets. Overall community composition also recovered to resemble uninvaded control plots in the years following *Rhododendron* removal. These findings present an encouraging message that at least some native communities can return naturally in the years following invasive species removal and may not require further management interventions to speed their return.

Keywords: Atlantic oak woodland, bryophytes, epiphytes, invasive species, restoration, *Rhododendron ponticum*.

1. Introduction

Invasive alien species are widely recognised as one of the major threats to worldwide native biodiversity (Genovesi 2005; Mooney 2005). Whilst an abundance of studies have investigated their impacts on aquatic communities, small mammals, insects and vascular plants, their impact on bryophyte communities has received little attention (Rothero 2003; Genovesi 2005; Mooney 2005). Indeed, bryophytes remain a relatively overlooked element in conservation strategies and their response to restoration measures is rarely considered (Rothero 2003; Long and Williams 2007). Understanding how bryophyte communities respond to invasive non-native species and revealing whether they recover following control efforts will be vital to ensuring the future of this diverse group (Rothero 2003; Long and Williams 2007).

The bryophyte community of Scottish Atlantic oak woodlands is particularly rich and is recognised as being of internationally significant conservation value (Rothero 2005; Long & Williams 2007; Porley and Hodgets 2005 pp164), as well as being listed in the EC Habitats Directive Annex 1 as "old sessile oakwoods with *Ilex* and *Blechnum* in the British Isles" (JNCC 2014). Invasion by non-native *Rhododendron ponticum* (hereafter *Rhododendron*) has been identified as one of the main threats to this habitat, since the characteristic humid climate and lack of temperature extremes which favour bryophyte diversity are also ideal for *Rhododendron* growth (Porley & Hodgets 2005,

pp165; Rothero 2005). Whilst there is clear evidence that *Rhododendron* invasion negatively impacts the understorey community (Cross 1975; Rotherham 1983; Maclean *et al.* 2017), there is little quantitative evidence for how it impacts the epiphytic community, including the diverse epiphytic bryophyte assemblage (Long & Williams 2007). Equally little is known about how this community responds to removal of the invasive stands, a practice which has increased dramatically in recent years following the discovery that *Rhododendron* serves as a host for *Phytophthera ramorum*, the fungus responsible for sudden oak death in trees, which also presents a significant economic threat to larch trees in Scotland (Edwards & Taylor 2008; Parrott & MacKenzie 2013). Addressing this key knowledge gap and elucidating how the epiphytic bryophyte community responds to *Rhododendron* invasion and subsequent control is therefore of vital importance to assessing the efficacy of Atlantic woodland conservation strategies (Long & Williams 2007; Parrott & MacKenzie 2013).

Invasion by *Rhododendron* leads to a well-documented decline in native understorey plant communities, which appears to be principally mediated through reduced light intensity under the dense stands (Cross 1975, Maclean *et al.* 2016). Since many epiphytic bryophytes are pre-adapted to low light conditions, this may facilitate their persistence during invasion (Porley & Hodgetts 2005 pp148; Kiraly et al. 2013). Additionally, it may be that epiphytic species can persist higher up the tree trunk, above the most severe impacts of the invading *Rhododendron,* leaving small source populations to recolonise down tree trunks once the *Rhododendron* has been removed (Zartman 2003; Pharo & Zartman 2006). The dense shading effect of *Rhododendron* is likely to be reduced

89 higher up the tree where light has less far to travel and can penetrate more easily
90 (Cross 1975). However, conditions higher up the trunk may be unsuitable
91 because of decreased humidity and increased exposure to temperature extremes
92 which may limit the ability of many epiphytic species to survive invasion by
93 retreating up the trunk in this manner (Porley & Hodgetts 2005). Indeed, since
94 mature *Rhododendron* bushes can attain heights of up to 8 m in wooded areas, it
95 is very possible that even epiphytes will be unable to tolerate their influence and
96 will become locally extinct in invaded areas (Edwards 2006). Many bryophytes
97 are reported to have limited dispersal capabilities, so it seems very likely that
98 once they have been lost in an area, recolonisation will take many decades (Miles
99 & Longton 1992; Snäll et al. 2003; Söderström & During 2005).

100 This study assessed the extent to which the epiphytic bryophyte
101 community of Atlantic oak woodland recovered following the effective removal
102 of invasive *Rhododendron* stands. To investigate this issue we utilised a series of
103 sites where dense *Rhododendron* stands had been removed between one and
104 thirty years ago. Using sites with up to thirty years of recovery following
105 *Rhododendron* removal to allow us to investigate the long-term consequences of
106 invasive species removal over ecologically relevant timescales. We used this
107 series of sites to address the questions: in the years following *Rhododendron*
108 clearance 1) does the total cover and species richness of the epiphytic plant
109 community return to levels similar to those found in uninvaded control sites?; 2)
110 does community composition return to a similar structure to that found in
111 uninvaded control sites?; and 3) do Atlantic species (which have highly restricted
112 European distributions and are of particular conservation importance) also
113 recover?

2. Methods

2.1 Data Collection

We identified and surveyed a series of 32 sites that were previously invaded by high density *Rhododendron* stands, but which had been cleared at different points in time between 1984 and 2013. We also surveyed 16 high *Rhododendron* density sites that have never been cleared and 16 uninvaded control sites for comparison with the cleared sites. Potential sites were identified following discussions with personnel at the regional Scottish Natural Heritage and Forestry Commission Scotland offices and meetings with local landowners with a substantial *R. ponticum* presence on their properties. Sites were chosen based on availability and also to ensure the even distribution of site types throughout the study area. Particular care was taken to ensure that dense *Rhododendron* and uninvaded control sites were fully interspersed with the cleared sites. This study design therefore conformed to the 'natural experiment' paradigm described by Diamond (1983), whereby site locations for experimental treatments (in this case uninvaded, dense or cleared *Rhododendron)* are determined by availability rather than following a strict experimental design with perfectly interspersed plots. This type of study is implemented due to constraints on conducting a strict experimental trial to answer the question under consideration (in this case the time constraint on the many decades necessary to grow and clear *Rhododendron* in an ideally designed field trial).

Sites were chosen to be as similar as possible to reduce variability not associated with their history of *Rhododendron* invasion. All survey sites were located on the west coast of Scotland in Atlantic oak woodlands around Argyll,

Kintyre and Lochaber, between 55°76' N and 56°90'. Atlantic oak woodlands are of high biodiversity value and are listed in Annex I of the EU Habitats Directive (old sessile oak woods with *Ilex* and *Blechnum* in the British Isles). Oak (*Quercus petraea* [Mattuschka] and *Q. robur* [Mattuschka]), and birch (*Betula pendula* [Roth] and *B. pubescens* Ehrh.) made up the majority of the tree community at all sites, with rowan (*Sorbus acuparia* L.), hazel (*Corylus avellana* L.), ash (*Fraxinus excelsior* L.), and holly (*Ilex aquifolium* L.) also occurring in moderate abundances. All sites consisted of ancient semi-natural woodland and were located more than 100 m from any ravines or plantation forestry and none were subject to active management of the tree community (i.e. no harvesting, coppicing or removal of dead wood). *Rhododendron* was removed from all the cleared sites by cutting the *Rhododendron* bushes at the base and applying herbicide (usually triclopyr or glyphosate; Edwards 2006), which represents the most common method of control currently used in Scotland (Edwards 2006). *Rhododendron* clearance was periodically maintained at all sites to prevent its return; however, no additional management interventions were applied at the sites.

At each site we established a 20 m by 20 m plot to sample the epiphyte community. It was decided to sample from this defined, limited area, rather than using randomly selected trees dispersed throughout the entire woodland site in order to keep the survey area the same between different sites and to ensure that the entire survey plot had been subject to dense *Rhododendron* cover prior to clearance. Dense *Rhododendron* cover was defined as being a mature stand featuring closed canopy cover across the survey plot. For cleared sites, specific plot locations within the greater woodland site were located following

discussions with the local land manager who could identify areas that had been subject to suitably dense *Rhododendon* cover prior to clearance.

To sample the epiphyte community, we randomly selected nine oak and nine birch trees within each plot to serve as sample trees. At a limited number of sites we were unable to identify nine trees of each species within the survey plot, in which case we extended the survey area to a 30 m by 30 m range. On the North-facing side of each sample tree we placed a 30 cm tall by 10 cm wide mini-quadrat at the base of the tree and also at breast height and recorded the total percent cover of every plant species present in the quadrat (principally mosses and liverworts, but occasionally including ferns and vascular species, especially at the tree base). Only the North-facing side of the trees was surveyed in order to maintain consistency between different trees, since the North side typically has a higher bryophyte abundance than the South side (Porley and Hodgets 2005). We therefore gathered survey data for four separate 'quadrat-types': birch at the tree base (birch lower), birch at breast height (birch upper), oak at the tree base (oak lower) and oak at breast height (oak upper).

Sites were split across ten spatial blocks with each block containing cleared, dense and uninvaded control sites. All surveys were conducted during summer 2014, apart from 13 uninvaded control site surveys and 11 dense *Rhododendron* surveys, which were conducted in summer 2013. These surveys were carried out in an identical manner and were used to supplement the 2014 dataset to maximise the uninvaded control and dense *Rhododendron* data that were available for analysis.

2.2 Statistical Analysis

189 Community composition data were averaged across the nine quadrats per
190 plot for each of the four quadrat-types, generating plot-level data for further
191 analysis. Total percent cover (sum of the percent cover for all species in the
192 quadrat) was also averaged across the nine quadrats per quadrat-type in each
193 plot. Species richness, however, was cumulatively summed across the nine
194 quadrats to give the total number of species recorded in each plot for each
195 quadrat-type. Total percent cover and species richness data were also calculated
196 for mosses only and liverworts only in addition to the calculations for all species
197 together.

198 Mixed effect models using spatial block as a random effect were then
199 fitted using the nlme package (Pinheiro *et al.* 2014) in R statistical software
200 (version 3.1.2; R Core Team 2014) to test the effect of *Rhododendron* site type
201 (dense *Rhododendron*, recently cleared sites (1-14 years since clearance), older
202 cleared sites (15-30 years since clearance) and uninvaded control sites on 1)
203 total percent cover and 2) species richness. Tukey's HSD was also calculated for
204 each of these comparisons to reveal which of the site types were significantly
205 different.

206 To investigate changes to overall community composition, partial-
207 Redundancy Analyses (partial-RDA, incorporating spatial block as a random
208 effect) were carried out for each quadrat-type using CANOCO 5 statistical
209 software (ter Braak & Šmilauer 2012). Since the data covered only a short
210 gradient of community composition, linear methods (rather than unimodal
211 methods) were used. Permutation tests (using 9999 permutations) were used to
212 test the significance of all constrained axes and data for each plot were
213 standardised by plot norm so that the analysis would reveal changes in the

proportion of each species and not be unduly influenced by changes in total vegetation cover between plots (Šmilauer & Lepš 2014). The same *Rhododendron* site types as in the previous analysis were used as a categorical explanatory variable (dense *Rhododendron*; uninvaded control; sites cleared 1-14 years ago; and sites cleared 15-30 years ago). A classified plot diagram (ter Braak & Šmilauer 2012) was then used to compare the community composition of plots falling into each *Rhododendron* site type to discover whether community composition was returning to that found in uninvaded control plots as time since *Rhododendron* clearance increased.

A second set of analyses was then carried out using data for Atlantic species only (following Hill & Preston 1998), in order to focus in on the response of these species of particular conservation interest. Mixed models and Tukey's HSD were utilised to investigate differences in total cover and species richness with *Rhododendron* site type. The Atlantic species present in our surveys were: mosses – *Dicranodontium denudatum* and *Dicranum scottianum*; liverworts - *Bazzania trilobata; Drepanolejeunea hamatifolia; Frullania tennerifae; Harpalejeunea molleri; Lejeunea patens; Lepidozia cupressina; Leptoscyphus cuneifolius; Microlejeunea ulcina; Plagiochila exigua; Plagiochila heterophylla; Plagiochila punctata; Plagiochila spinulosa* and *Scapania gracilis*, and ferns - *Hymenophyllum tunbrigense* and *Hymenophyllum wilsonii.* Whilst the 'Atlantic species' designation is typically limited to bryophytes, it was decided to include the two filmy ferns in our analysis since they have similar distributions to the Atlantic bryophytes and are considered species of interest in Atlantic oak woodland (Long & Williams 2007). A species-enivronmental variables (i.e. *Rhododendron* site type) biplot was then created from the previously constructed

RDA to look at the response of Atlantic community composition to *Rhododendron* clearance. Whilst this analysis utilised data for all species (so that the complete community would be taken into account when calculating the relationships between plots in each treatment), only Atlantic species were then highlighted in the resulting graph to reveal how they responded to *Rhododendron* clearance.

3. Results

Over the entire study, 63 different species were recorded, comprising 29 species of moss, 26 liverworts, 3 ferns and 5 vascular species (vascular species were very occasionally present in quadrats located at the tree base). A total of 55 species were recorded on birch trees and a total of 59 species on oak trees. Average percent cover across the study was 66%, with an average of 62% for birch lower quadrats, 51% for birch upper quadrats, 82% for oak lower quadrats and 71% for oak upper quadrats.

3.1 Question 1: Does the total cover and species richness of the epiphytic plant community return to similar levels found in uninvaded control sites?

Overall percent cover did not show any significant differences between the *Rhododendron* site types for birch lower ($F_{3,51}$ = 2.52, P = 0.069), birch upper ($F_{3,51}$ = 1.22, P = 0.313) or oak upper ($F_{3,51}$ = 1.53, P = 0.219) quadrats, but recently cleared sites were revealed to have a lower epiphyte cover than uninvaded control sites for oak lower quadrats ($F_{3,51}$ = 3.44, P = 0.023) (Fig. 1). Separate analyses of moss and liverwort cover, however, revealed that significant changes in liverwort cover were being masked by opposing changes in moss cover to result in this lack of change in the percent cover of all species

for most quadrat types. Tukey's HSD revealed that dense sites had significantly lower liverwort cover than uninvaded control sites for both birch ($t_{3,51}$ = 3.10, P = 0.016) and oak ($t_{3,51}$ = 3.29, P = 0.010) lower quadrats, but not for the upper quadrats (birch: $t_{3,51}$ = 0.71, P = 0.891; oak: $t_{3,51}$ = 1.23, P = 0.610). Recently cleared sites did not have significantly different liverwort cover from dense sites (birch lower: $t_{3,51}$ = 1.16, P = 0.653; birch upper: $t_{3,51}$ = 0.28, P = 0.992; oak lower: $t_{3,51}$ = 0.78, P = 0.862; oak upper: $t_{3,51}$ = 0.16, P = 0.877), but older cleared sites (15 – 30 years since clearance) had a significantly higher liverwort cover than dense sites for all four quadrat types (birch lower: $t_{3,51}$ = 6.16, P < 0.001; birch upper: $t_{3,51}$ = 3.17, P = 0.013; oak lower: $t_{3,51}$ = 5.59, P < 0.001; oak upper: $t_{3,51}$ = 4.07, P < 0.001). Indeed, older cleared sites attained a significantly higher liverwort cover than uninvaded control sites all quadrat types apart from oak lower (birch lower: $t_{3,51}$ = 3.25, P = 0.011; birch upper: $t_{3,51}$ = 4.16, P < 0.001; oak lower: $t_{3,51}$ = 2.02, P = 0.194; oak upper: $t_{3,51}$ = 2.67, P = 0.049). Whilst the glms revealed no significant differences for moss cover in any quadrat type (birch lower: $F_{3,51}$ = 1.99, P = 0.128; birch upper: $F_{3,51}$ = 1.37, P = 0.261; oak lower: $F_{3,51}$ = 1.50, P = 0.225; oak uper: $F_{3,51}$ = 1.83, P = 0.153), the general pattern was for dense sites to have the highest cover, followed by uninvaded control sites, with both recent and older cleared sites having the lowest cover. These trends were opposite to the significant differences observed in liverwort cover and suggest that the lack of change in overall cover masked the replacement of mosses with liverworts as time since *Rhododendron* removal increased.

Analysis of differences in epiphyte species richness revealed very similar patterns to those found for percent cover (Fig. 2). Tukey's HSD revealed that

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older cleared sites showed significantly higher liverwort species richness than dense *Rhododendron* sites (birch lower: $t_{3,51} = 5.58$, $P < 0.001$; birch upper: $t_{3,51} = 3.05$, $P = 0.019$; oak lower: $t_{3,51} = 3.91$, $P = 0.002$; oak upper: $t_{3,51} = 3.44$, $P = 0.006$), whereas recently cleared sites were not significantly different from dense sites for all four quadrat types (birch lower: $t_{3,51} = 1.78$, $P = 0.294$; birch upper: $t_{3,51} = 1.46$, $P = 0.467$; oak lower: $t_{3,51} = 0.31$, $P = 0.781$; oak upper: $t_{3,51} = 1.15$, $P = 0.663$). Older cleared sites also showed significantly higher liverwort species richness than uninvaded control sites for both lower quadrats (birch: $t_{3,51} = 3.08$, $P = 0.017$; oak: $t_{3,51} = 3.51$, $P = 0.005$), but not the upper quadrats (birch: $t_{3,51} = 2.04$, $P = 0.188$; oak: $t_{3,51} = 1.46$, $P = 0.469$). Again, the glms revealed no significant differences in moss species richness between *Rhododendron* site types (birch lower: $F_{3,51} = 0.69$, $P = 0.561$; birch upper: $F_{3,51} = 1.35$, $P = 0.268$; oak lower: $F_{3,51} = 2.05$, $P = 0.119$; oak upper: $F_{3,51} = 0.40$, $P = 0.749$), but in contrast to the percent cover analyses, this did not act in opposition to the trends in liverwort species richness, resulting in significant differences in overall epiphyte species richness between the different *Rhododendron* site types for all four quadrat types (birch lower: $F_{3,51} = 5.24$, $P = 0.003$; birch upper: $F_{3,51} = 5.03$, $P = 0.004$; oak lower: $F_{3,51} = 6.05$, $P = 0.001$; oak upper: $F_{3,51} = 2.78$, $P = 0.049$).

3.2 Question 2: Does community composition return to a similar structure to that found in uninvaded control sites?

The partial-RDAs (Fig. 3) demonstrated a significant impact of *Rhododendron* site type on epiphyte community composition (birch lower: $F = 3.3$, $P < 0.001$; birch upper: $F = 2.1$, $P = 0.002$; oak lower: $F = 2.3$, $P = 0.002$; oak

upper: F = 1.9, P = 0.006). They revealed that community composition in uninvaded control plots (UC) was predictably different from that in dense *Rhododendron* plots (DR). However, there was a degree of overlap in the space occupied by plots belonging to these two groups in the diagrams, revealing that many similarities remain between the epiphyte community in dense *Rhododendron* and uninvaded control plots. The analyses also revealed a definite recovery in community composition as time since *Rhododendron* control increased, with plots cleared less than 15 years ago largely occurring to the right of the diagrams, close to the dense *Rhododendron* plots, and plots cleared 15 to 30 years ago largely occurring to the left of the diagrams, close to the uninvaded control plots. However, there was substantial overlap between the different groups, demonstrating that although community composition did change as time since *Rhododendron* clearance increased, the different communities were still fairly similar and there was not a complete turnover in community composition between the different plot types.

3.3 Question 3: Do Atlantic species recover as readily as more widely distributed species?

A complete list of all the Atlantic species present in each *Rhododendron* site type is available in the Supporting Information (Tables S1 and S2). The glms revealed that *Rhododendron* site type had a significant impact on the percent cover and species richness of Atlantic species for all four quadrat types (percent cover: birch lower: $F_{3,51} = 7.94$, $P < 0.001$; birch upper: $F_{3,51} = 3.19$, $P = 0.031$; oak lower: $F_{3,51} = 8.17$, $P < 0.001$; oak upper: $F_{3,51} = 3.85$, $P = 0.015$: species richness: birch lower: $F_{3,51} = 10.02$, $P < 0.001$; birch upper: $F_{3,51} = 3.74$, $P = 0.017$; oak

lower: $F_{3,51} = 7.35$, $P < 0.001$; oak upper: $F_{3,51} = 6.61$, $P < 0.001$) (Fig. 4). Tukey's HSD revealed that recently cleared sites were not significantly different from dense *Rhododendron* sites for either percent cover (birch lower: $t_{3,51} = 1.06$, $P = 0.715$; birch lower: $t_{3,51} = 0.83$, $P = 0.839$; oak lower: $t_{3,51} = 0.33$, $P = 0.879$; oak upper: $t_{3,51} = 0.44$, $P = 0.862$) or species richness (birch lower: $t_{3,51} = 1.85$, $P = 0.265$; birch upper: $t_{3,51} = 1.78$, $P = 0.296$; oak lower: $t_{3,51} = 0.78$, $P = 0.763$; oak upper: $t_{3,51} = 1.12$, $P = 0.680$). Older cleared sites, however, showed significantly higher percent cover (birch lower: $t_{3,51} = 4.66$, $P < 0.001$; birch upper: $t_{3,51} = 2.94$, $P = 0.025$; oak lower: $t_{3,51} = 4.39$, $P < 0.001$; oak lower: $t_{3,51} = 2.75$, $P = 0.035$) and species richness (birch lower: $t_{3,51} = 5.42$, $P < 0.001$; birch upper: $t_{3,51} = 3.33$, $P = 0.009$; oak lower: $t_{3,51} = 3.92$, $P = 0.002$; oak upper: $t_{3,51} = 4.14$, $P < 0.001$) than dense sites, suggesting that Atlantic species recovered well following the removal of invasive *Rhododendron*. Indeed, for birch lower quadrats, older cleared sites actually attained a higher Atlantic species richness than uninvaded control sites ($t_{3,51} = 3.02$, $P = 0.020$), and this pattern was repeated for the other quadrat types, though the differences were not significant (birch upper: $t_{3,51} = 1.77$, $P = 0.298$; oak lower: $t_{3,51} = 1.19$, $P = 0.638$; oak lower: $t_{3,51} = 1.43$, $P = 0.488$).

The partial-RDAs (Fig. 5) revealed that Atlantic species had a strong aversion to dense *Rhododendron* plots (DR) and were more likely to be found in uninvaded control (UC) and cleared (1-14 and 15-30) plots for all quadrat types apart from birch upper, which did feature several Atlantic species in the dense *Rhododendron* plots. An affinity of *Drepanolejeunea hamatifolia* for dense *Rhododendron* plots was also observed in the oak lower quadrats. The centroid for uninvaded control (UC) and older cleared plots (15-30) were very close for

362 the lower quadrats, highlighting that these site types feature very similar
363 communities and that recovery has been largely successful. These centroids
364 were further apart for the upper quadrats (though still at the same side of the
365 diagram), suggesting that recovery has been less complete in these quadrats.
366 However, this may also be driven by the larger degree of overlap between
367 recently cleared sites (1-14) and uninvaded controls for these upper quadrats
368 (Fig. 3).

369

370 **4. Discussion**

371 The epiphytic plant community, which was principally comprised of
372 bryophytes, recovered well in the years following *Rhododendron* clearance,
373 showing substantial increases in both total vegetation cover and species richness
374 by 15 to 30 years following clearance. This recovery applied equally to Atlantic
375 species as to more widespread species. Ordinations revealed that whilst dense
376 *Rhododendron* caused a slight shift in community composition away from that
377 found in uninvaded control plots, the community appeared to be reconverging
378 on the composition found in uninvaded control plots after 15 to 30 years of
379 recovery following effective *Rhododendron* clearance. These results therefore
380 suggest that epiphytic plants of Scottish Atlantic oak woodlands are relatively
381 resilient to the long-term effects of invasive *Rhododendron*. Whilst invaded sites
382 showed reductions in epiphytic plant species richness, cleared sites could be,
383 ultimately, as rich and diverse as pristine, uninvaded woodlands.

384

4.1 Question 1: Does the total cover and species richness of the epiphytic plant community return to similar levels found in uninvaded control sites?

Rhododendron invasion had unexpectedly little impact on the overall percent cover of epiphytic species, with no significant differences being found between densely invaded plots, older cleared plots and uninvaded controls. Greater impacts were observed for species richness than for percent cover, however, with older cleared sites having significantly higher species richness than densely invaded sites. Whilst dense plots were revealed to have lower species richness than uninvaded controls, these differences were not significant due to considerable variation between plots of the same *Rhododendron* type. This lack of a significant difference between dense and uninvaded plots for both cover and species richness was surprising given the dramatic decreases in the cover of understorey species during *Rhododendron* invasion (Cross 1975; Maclean *et al.* 2017), and the high concern in the conservation literature that *Rhododendron* invasion is detrimental to epiphytic bryophytes (Long and Williams 2007). Since epiphytic bryophytes are typically adapted to the reduced light levels and higher humidity found under tree canopies, it may be that they are better able to survive further light reductions caused by invasive shrubs compared to the vascular species examined in most studies (Porley & Hodgets 2005 pp148; Kiraly *et al.* 2013; Maclean *et al.* 2017). Indeed, there are concerns that the dramatic changes to light intensity and humidity caused by removing the invasive *Rhododendron* stands may damage any surviving bryophytes (Long & Williams 2007; see also Dynesius & Hylander 2007). Whilst leaving dead *Rhododendron* stems in place may help to mitigate this impact and facilitate restoration (Long & Williams 2007; Parrott & MacKenzie 2013), our study revealed that even in the

absence of these enhanced management measures, the epiphytic bryophyte community was able to recover well in 15 to 30 years.

Partitioning the results to look separately at mosses and liverworts, revealed that large impacts to liverwort cover and species richness were being partially masked by reduced impacts on mosses. Liverworts showed significantly lower cover in dense than uninvaded plots for the lower quadrats. They also underwent dramatic increases in both cover and species richness with increasing time since *Rhododendron* clearance, with older cleared sites (15-30 years) featuring the same or higher cover and species richness than uninvaded controls. This higher liverwort cover and species richness in plots with 15-30 years since clearance than in uninvaded control plots was surprising. It may be that some feature of cleared sites, such as a lack of competition with vascular plants, particularly at the tree base, may have benefitted the liverwort communities. Alternatively, it may be that our uninvaded control sites were not as directly comparable with our cleared sites as hoped. Whilst a great deal of care was taken to select sites that would be directly comparable, it may be that certain features that facilitated *Rhododendron* growth, such as high humidity, also made these sites particularly favourable to liverwort growth. Since it is impossible to know what communities were present at these sites prior to invasion (which occurred many decades ago), comparison with uninvaded sites represented the only available baseline against which to assess recovery. In any case, the high liverwort cover and species richness at older cleared sites highlights the conservation potential of these areas and emphasises the importance of ensuring that cleared sites remain *Rhododendron*-free.

434 The rapid recovery in liverwort species richness indicated that, whilst
435 dense *Rhododendron* stands were detrimental to liverwort cover, species were
436 able to quickly recover their former abundance following clearance. It is possible
437 that the native liverworts were able to persist higher up the tree during invasion,
438 so avoiding the most severe impacts of the *Rhododendron*. Similar niche shifts
439 along canopy height were seen following the disturbance caused by forest
440 fragmentation in Amazonian forests (Zartman 2003; Pharo & Zartman 2006).
441 The higher liverwort cover in upper quadrats than lower quadrats in dense
442 *Rhododendron* plots found in our study would support the presence of upper
443 canopy refugia, but unfortunately logistical constraints precluded sampling high
444 into the canopy. In addition to surviving higher up the trees, small pockets of
445 diversity may have persisted on individual trees growing in small gaps in the
446 invasive *Rhododendron* thickets. Whilst we know of no other studies addressing
447 the impact of invasive plants on epiphyte diversity, studies considering the
448 impacts of other disturbances such as forest fragmentation and clear-felling
449 showed mixed benefits of small, isolated refugia, with beneficial effects
450 demonstrated in some studies (Dynesius & Hylander 2007; Toledo-Aceves *et al.*
451 2014), and no benefit shown in other cases (Lohmus, Rosenvald & Lohmus 2006;
452 Perhans *et al.* 2009).

453 Whilst all our cleared plots were located in areas that originally hosted
454 very dense *Rhododendron* stands, the total extent and configuration of these
455 stands will undoubtedly have differed with respect to their ability to provide
456 effective refugia. This variation in the presence of refugia, or in the distance to
457 the nearest uninvaded woodland, may explain much of the variation seen in our
458 results between plots in the same *Rhododendron* category. Another potential

source of variation may have been the duration of invasion prior to clearance, which was always long enough to provide mature, dense *Rhododendron* cover, but may have differed by several years or decades between sites. Unfortunately the lack of a detailed history of *Rhododendron* spread at the majority of sites prevented using this information as an additional explanatory variable in our analyses.

Mosses, in contrast to liverworts, showed very few significant changes through time, and did not demonstrate uncharacteristically low levels of cover or species richness in the dense *Rhododendron* plots. This suggested that they were better able to persist under the dense *Rhododendron* stands and maintain typical levels of cover during the invasion. Observations in the field supported these findings, with trees under dense *Rhododendron* canopy often featuring a moderate cover of common mosses such as *Isothecium myosuroides* or *Hypnum cupressiforme*. Whilst these populations were typically etiolated and pale and rarely bore sporophytes (J. Maclean, pers. obs.), it seems they served to effectively maintain a foothold for many species in the face of invasion.

4.2 Question 2: *Does community composition return to a similar structure to that found in uninvaded control sites?*

Ordination revealed that the community composition of epiphytic plants in plots where *Rhododendron* was cleared 15 to 30 years ago was very similar to that of uninvaded control plots, suggesting that site recovery had been largely successful. This recovery was particularly effective for the lower quadrats, although substantial overlap was also detected between cleared sites and uninvaded control sites for the upper quadrats. Oak upper quadrats in particular

484 may require a longer period of recovery to achieve the community composition
485 found in uninvaded controls. Differences in community composition, however,
486 were fairly slight, even between uninvaded control and dense *Rhododendron*
487 plots, which exhibited some degree of overlap in all four quadrat types (birch
488 and oak, tree base and breast height). A relatively short gradient in community
489 composition (between 2.1 and 2.7 units), which supported the use of linear
490 rather than univariate ordination techniques, also suggested that the plots did
491 not exhibit a high degree of community turnover and had many species in
492 common. This similarity in the epiphytic community between dense, cleared and
493 uninvaded sites contrasts the large differences seen in the understorey
494 community and emphasises that different communities within a site may
495 respond very differently to both the arrival and the removal of invasive species
496 (Maclean *et al.* 2017).

497 The successful recovery of native species following invasive species
498 removal is a relatively rare occurrence (Reid *et al.* 2009; Corbin & D'Antonio
499 2012), although it has been reported in some cases (Patten & O'Casey 2007; Rey
500 Benayas *et al.* 2009). To our knowledge, this is the first study to investigate the
501 impact of invasive plant removal on the native epiphyte community, and it was
502 encouraging to discover a healthy native epiphytic plant community in sites that
503 had been *Rhododendron*-free for at least 15 years. It should be noted that we only
504 recorded plant species in our surveys and did not monitor other important
505 components of the epiphytic community such as lichens. Further study will be
506 necessary to reveal how lichens respond to *Rhododendron* invasion and
507 clearance and it cannot be assumed that they will show the same patterns of
508 recovery as the species investigated in this study. Since the majority of the

epiphytic plant community in our study area consisted of bryophytes (supplemented by some ferns and a few understory vascular species at the tree base), this recovery relied on the ability of bryophytes to survive the invasion in low numbers and increase their populations effectively after the *Rhododendron* had been cleared. This ability of bryophytes to recover following *Rhododendron* clearance is supported by research revealing that bryophytes in the understorey also recover well following *Rhododendron* clearance, whereas forbs and grasses do not (Maclean *et al.* 2017).

As discussed in the previous section, it is possible that small bryophyte populations were able to persist in refugia higher up the trees, or on isolated trees growing in spots of reduced *Rhododendron* density (Zartman 2003; Dynesius & Hylander 2007). The ability of epiphytic bryophytes to increase their populations and spread rapidly from such refugia is a highly debated topic (Pharo & Zartman 2007). Studies that directly measure spore dispersal have found that a vast majority of spores remain within a few centimetres of the parent plant (Miles & Longton 1992; Porley & Hodgets 2005), and bryophytes are typically reported as being highly dispersal limited (Snäll *et al.* 2003; Söderström & During 2005). This, however, runs in contrast to evidence that bryophytes can occasionally disperse very long distances, giving rise to distributions that span multiple continents (Porley & Hodgets 2005 pp74; Pharo & Zartman 2007). Additionally, some studies have discovered high rates of community turnover, for example discovering large differences in bryophyte community composition between different seasons of the same year, which suggest an ability to spread rapidly when conditions are favourable (Scott 1971; Ross-Davis & Frego 2004). Indeed, the ability of most bryophytes to reproduce

by forming a new plant from a detached fragment of leaf or stem, in addition to the production of sexual spores or specialised asexual propagules (gemmae), is likely to facilitate their ability to spread over moderate distances (Porley & Hodgets pp77). Altogether, our results showing a healthy community 15-30 years after removal suggests that most species were able to recover effectively and increase their coverage in the years following *Rhododendron* removal.

4.3 Question 3: Do Atlantic species recover as readily as more widely distributed species?

The Atlantic species present in our study (incorporating two mosses, thirteen liverworts and two filmy ferns) showed dramatic increases in both total cover and species richness as time since *Rhododendron* clearance increased. These increases culminated in plots where *Rhododendron* was cleared 15 or more years ago achieving levels of cover and species richness that were indistinguishable from, or in the case of birch lower species richness, significantly higher than, uninvaded control plots. The partial-RDA revealed that Atlantic species were present in their highest abundances in cleared and uninvaded plots, and the similarity between older (15-30 years) cleared and uninvaded plots suggested that Atlantic species were able to recover following *Rhododendron* removal, particularly in the lower quadrats (Fig. 5). In contrast, dense *Rhododendron* was highly unfavourable to Atlantic species, with the vectors for almost all Atlantic species clustering away from the dense *Rhododendron* plots, although some appeared to show an affinity for the dense *Rhododendron* plots in birch upper quadrats. It is therefore clear that

559 *Rhododendron* invasion was highly detrimental to Atlantic bryophytes, although
560 its effective removal appears sufficient to counter much of its negative impact
561 and further management interventions are unlikely to be required for the
562 species present in our study.

563 Our results have revealed that the Atlantic species in our dataset, which
564 consisted principally of liverworts, responded to *Rhododendron* removal in a
565 similar way to the liverwort community as a whole. Since Atlantic species are
566 defined by their distribution rather than on ecological grounds, there would be
567 no strong reason to expect them to respond any differently from non-Atlantic
568 species to disturbances such as plant invasions (Ratcliffe 1968; Porley & Hodgets
569 2005 pp83). However, since an Atlantic distribution is in most cases
570 underpinned by a requirement for relatively consistent moisture availability
571 throughout the year (Ratcliffe 1968; Porley & Hodgets 2005 pp83), it could be
572 supposed that Atlantic species would be more vulnerable to the rapid changes in
573 humidity caused by removing dense *Rhododendron* thickets (Long & Williams
574 2007). Indeed, invasive *Rhododendron* has often been cited as one of the major
575 threats to Atlantic bryophyte conservation, but critical information on their
576 recovery following *Rhododendron* clearance was lacking (Long & Williams 2007;
577 Scottish Natural Heritage 2007; Edwards & Taylor 2008). It is therefore highly
578 encouraging that our study has revealed that Atlantic species recover well
579 following *Rhododendron* clearance, so long as the site remains *Rhododendron*-
580 free. We wish to highlight, however, that we used general, untargeted surveys in
581 our analysis and only monitored oak and birch trees due to the logistical
582 constraints of monitoring all the tree species present in Atlantic oak woodland.
583 These surveys therefore capture only the responses of regionally abundant

584 epiphytes of oak and birch and further targeted surveys will be necessary to fully
585 assess the impact of *Rhododendron* invasion on rare species of particular
586 conservation interest. It was encouraging to find *Plagiochila heterophylla* in one
587 cleared and two dense *Rhododendron* plots (in addition to three uninvaded
588 controls), however, suggesting that this rare though locally frequent Atlantic
589 bryophyte can still be found following *Rhododendron* invasion.
590
591
592 *4.4 Conclusions*

593 Invasive *Rhododendron* stands cause widely reported declines in native
594 plant communities (Cross 1975; Rotherham 2001; Scottish Natural Heritage
595 2007). Whilst most previously published scientific research has focussed on
596 impacts to vascular plants (see for example Cross 1975; Rotherham 1983; Nilsen
597 *et al.* 2001; Maclean *et al.* 2017), our study supports abundant qualitative
598 observations that dense *Rhododendron* causes a decrease in the cover and
599 species richness of epiphytic bryophytes, with liverworts being particularly
600 affected (Long & Williams 2007; Parrott & MacKenzie 2013). Our research went
601 further, however, to investigate for the first time how the native epiphytic plant
602 community responded to the removal of this invasive shrub. We revealed that
603 total cover and species richness increased dramatically in the years following
604 *Rhododendron* removal, with overall community composition recovering
605 successfully to resemble that of uninvaded control plots. Altogether, our results
606 provide a message of encouragement that this important component of
607 internationally renowned Atlantic oak woodlands is able to recover without any

608 further management interventions following the removal of invasive
609 *Rhododendron*.
610

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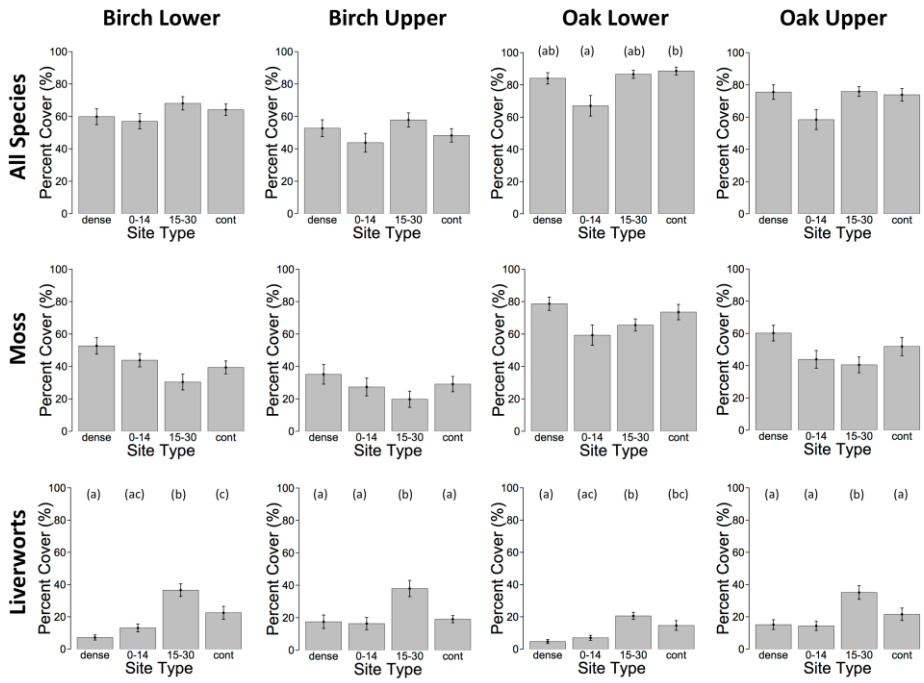

Fig. 1: The difference in percent cover of all species (row 1), mosses (row 2), and liverworts (row 3) between different *Rhododendron* site types. Site types are dense *Rhododendron* (dense), recently cleared sites (0-14 years since clearance), sites that have been clear from *Rhododendron* for a longer period of time (15-30 years since clearance) and uninvaded control plots (cont). Letters above each graph show significant differences ($P < 0.05$) between site types as revealed by Tukey's HSD test. Graphs with no letters have no significant differences between the site types. Error bars show standard errors.

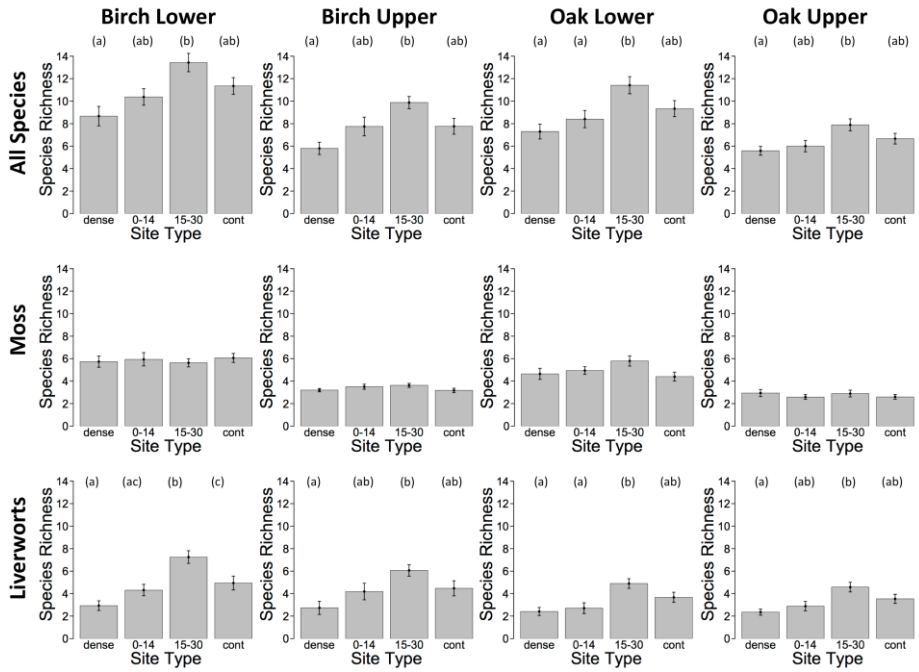

Fig. 2: The difference in species richness of all species (row 1), mosses (row 2), and liverworts (row 3) between different *Rhododendron* site types. Site types are dense *Rhododendron* (dense), recently cleared sites (0-14 years since clearance), sites that have been clear from *Rhododendron* for a longer period of time (15-30 years since clearance) and uninvaded control plots (cont). Letters above each graph show significant differences ($P < 0.05$) between site types as revealed by Tukey's HSD test. Graphs with no letters have no significant differences between the site types. Error bars show standard errors.

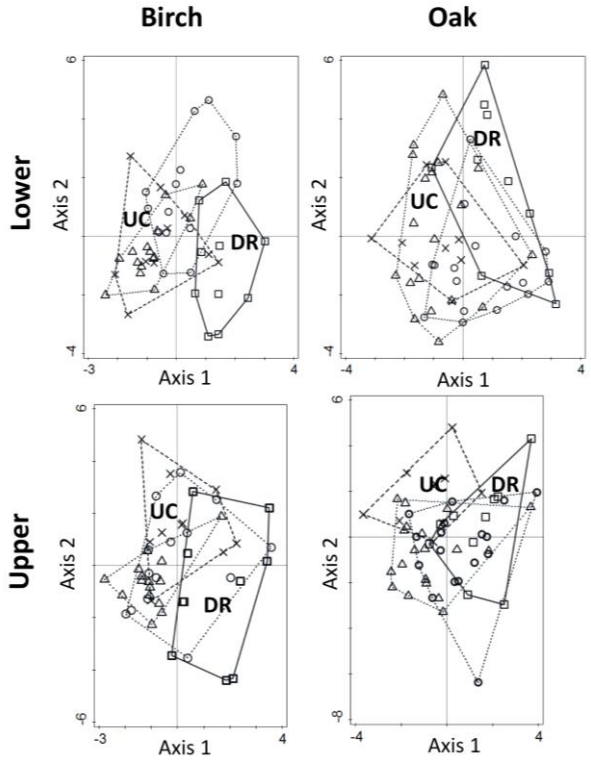

Fig. 3: Differences in community composition between different *Rhododendron* sites types. Classified plot diagrams from the partial-RDA looking at the effect of *Rhododendron* site type on community composition. The shapes delineate the extent of the plots belonging to the same *Rhododendron* site type. Sites with dense *Rhododendron* = DR (□, ——); uninvaded control sites = UC (×, ----); plots cleared 1-14 years ago = (○, ····); plots cleared 15-30 years ago = (Δ, ····).

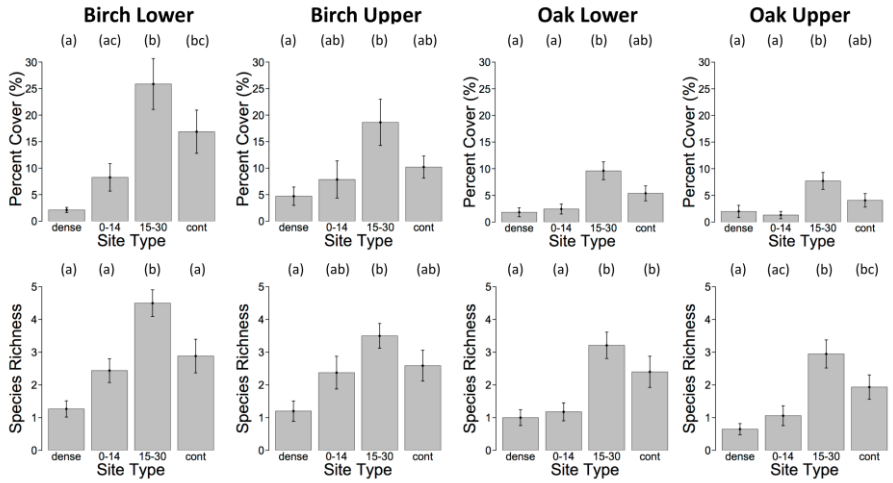

Fig. 4: The difference in percent cover (row 1) and species richness (row 2) for Atlantic species in the different *Rhododendron* site types. Site types are dense *Rhododendron* (dense), recently cleared sites (0-14 years since clearance), sites that have been clear from *Rhododendron* for a longer period of time (15-30 years since clearance) and uninvaded control plots (cont). Letters above each graph show significant differences ($P < 0.05$) between site types as revealed by Tukey's HSD test. Error bars show standard errors.

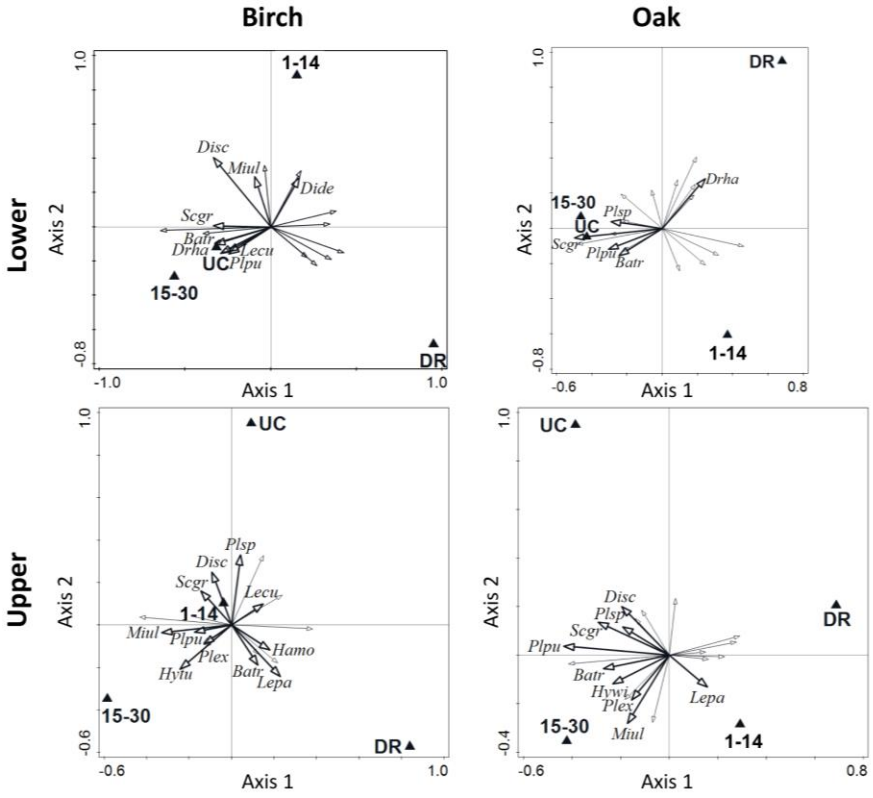

Fig. 5: Response of Atlantic species to *Rhododendron* treatment. The graphs show the results of partial-RDAs revealing the affinity of different atlantic species for plots with dense *Rhododendron* (DR), plots where *Rhododendron* had been cleared 1-14 or 15-30 years previously, and uninvaded control plots (UC). Triangles show the centroid of the scores for plots belonging to that *Rhododendron* site type. Atlantic species only are identified to make the plots clearer (these graphs are presented with all species labelled in the Supporting Information). Atlantic species showed a clear preference for cleared and uninvaded control plots. Species are: ***Batr –*** *Bazzania trilobata;* ***Dide –*** *Dicranodontium denudatum;* ***Disc*** *- Dicranum scottianum;* ***Drha*** *- Drepanolejeunea hamatifolia;* ***Hamo –*** *Harpalejeunea molleri;* ***Hywi*** *– Hymenophyllum wilsonii;* ***Lecu –*** *Lepidozia cupressina;* ***Lepa*** *– Lejeunea patens;* ***Miul –*** *Microlejeunea ulcina;* ***Plex –*** *Plagiochila exigua;* ***Plpu –*** *Plagiochila punctata;* ***Plsp –*** *Plagiochila spinulosa;* ***Scgr –*** *Scapania gracilis.*